

Mass spawning of corals on Western Australian reefs and comparisons with the Great Barrier Reef

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Abstract

Multispecific, synchronous spawning or 'mass spawning' of scleractinian corals on Western Australian reefs was observed fortuitously in the Dampier Archipelago in March 1984. Subsequent studies during 1985-1988 have documented this phenomenon along the Western Australian coastline on tropical and temperate coral reefs and spawning has been observed to occur simultaneously on reefs separated by over 12 degrees of latitude. Mass spawning occurred mainly around the third quarter of the moon (*ie* 7-9 nights after the full moon) on neap, nocturnal, ebb tides. Although most of the corals studied spawned after the full moon in March each year, in some years, some spawned on the same nights after the full moon in April. Studies since 1988 have shown that a small percentage of corals spawn after the full moons in February and April each year.

As a result of these studies, 102 species of scleractinian corals from Western Australian reefs are now known to spawn during the austral autumn. A further 44 species were found to contain ripe gonads during the same period and are presumed to participate in the annual coral mass spawning on Western Australian reefs. These records represent 88% of the coral species studied so far or about 46% of the coral species currently described from Western Australia.

In Western Australia, coral mass spawning coincides approximately with the annual intensification of the Leeuwin Current, a warm poleward current of tropical origin that flows unidirectionally along the coastline of Western Australia during the austral autumn and winter. This current provides a mechanism for the southward dispersal of planulae and raises the possibility of a unidirectional gene flow between regionally separate coral reefs in Western Australia.

Comparisons with the spring coral mass spawnings on the Great Barrier Reef indicate that, apart from the seasonal difference in the timing of spawning, many similarities exist suggesting that the same phenomenon is occurring on both sides of Australia. Comparisons of annual sea temperature patterns however, both within Western Australia and between the east and west coasts of tropical Australia, suggest that sea temperature is not a proximate or ultimate factor in determining the breeding season of scleractinian corals. It is postulated that the different seasonal timing of coral mass spawning on the east and west coasts of Australia is the result of an endogenous rhythm reflecting the breeding patterns of ancestral corals as a consequence of selective dispersal of larvae from equatorial regions.

The simultaneous spawning of many other coral reef invertebrates during the coral mass spawnings suggests that the findings presented here in relation to scleractinian corals have important implications regarding the reproductive patterns of many other coral reef animals.

Introduction

The recent discovery of multispecific, synchronous spawning or 'mass spawning' of tropical reef corals on the Great Barrier Reef and on Western Australian reefs has greatly increased our understanding of the reproductive patterns of many scleractinian corals (Harrison *et al.* 1983, Harrison *et al.* 1984, Simpson 1985, 1987, Babcock *et al.* 1986). In contrast to the brief, predictable spawning periods of corals on the Great

Barrier Reef and on Western Australian reefs, corals in the Red Sea exhibit temporal reproductive isolation (Shlesinger & Loya 1985) indicating that the reproductive traits of reef corals are highly variable. The proximate (environmental) and ultimate (ecological) factors responsible for these reproductive patterns are poorly understood. As pointed out by Willis *et al.* (1985), comparisons of the reproductive patterns of corals between geographic regions may

identify common factors that will possibly pinpoint underlying causes of the mass spawning phenomenon.

Following the fortuitous discovery of coral mass spawning in the Dampier Archipelago (Fig. 1) during March 1984, studies at the same location in 1985 confirmed that coral mass spawning occurred during a brief predictable period after the full moon in March. The coral species involved were documented and aspects of the physical environment during the spawning period were characterised (Simpson 1985). Similar studies at the Dampier Archipelago and the Ningaloo Reef in 1986 confirmed that coral spawning at these two locations occurred synchronously, and studies at the Abrolhos Islands in March 1987 determined that coral mass spawning on these temperate reefs occurred at approximately the same time as on tropical reefs in Western Australia (Simpson & Masini 1986, Simpson 1987). In addition, volunteer observers were stationed along the coastline of Western Australia in March 1987 and 1988 to determine the extent of coral spawning synchrony within and between regionally separate coral reefs in Western Australia (Simpson 1988).

In this paper I summarise the results of coral mass spawning studies on Western Australian reefs between 1985 and 1988 and draw comparisons with the spring mass spawnings on the Great Barrier Reef. An hypothesis explaining the difference in the seasonal timing of the breeding seasons of scleractinian corals on the east and west coasts of Australia is also outlined.

Methods

Polyp reproductive status was determined by the presence of pigmented eggs either by examination of freshly broken pieces of live coral in the field or under a dissecting microscope in the laboratory. In addition to ripe eggs, the presence of testes and motile sperm with condensed heads were used as criteria for reproductive maturity (Harrison *et al.* 1984). Spawning of corals in the field was determined directly by observation of gamete release *in situ*, the appearance of eggs on the sea surface, or inferred from the disappearance of mature gametes in sequential samples from tagged colonies.

In most years 200+ coral colonies were tagged in the two weeks before the predicted time of spawning and their reproductive status was determined by the methods outlined above. The reproductive status of a representative subset of these colonies, usually numbering about 30-50, was monitored daily. Random collections were also made during the week before and after spawning. Untagged species observed to be spawning during night dives were also recorded or collected. In general, night observations were carried out between sunset and about 2230 h on about 6 nights around the time of predicted spawning, usually 6-11

nights after the full moon. In earlier years searches for coral eggs floating on the sea were made on several nights either side of these dates, usually between sunset and 2100 h. These combined observations, together with the daily monitoring of tagged colonies, ensured that spawning dates were determined accurately.

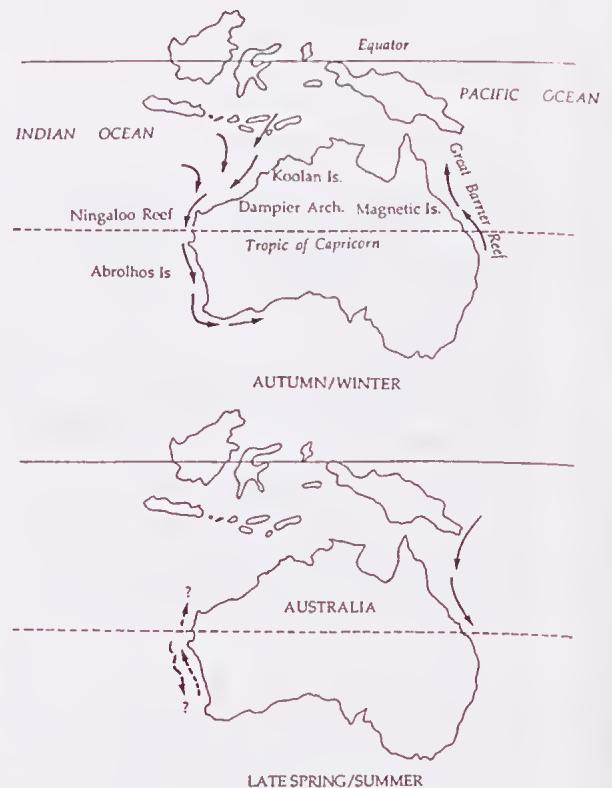


Figure 1 Seasonal variation in the drift of surface waters on the east and west coasts of Australia. The change from a variable or northerly drift to a net southerly drift occurs around March on the west coast and around November on the east coast and coincides approximately with the timing of coral mass spawning at both locations.

Details of the species and number of colonies that were sampled in the Dampier Archipelago in November 1984 and March 1985 can be found in Simpson (1985). In 1986, 512 colonies from at least 74 species were sampled at the Dampier Archipelago and the Ningaloo Reef (Simpson, unpublished data). In 1987, 422 colonies from 107 species were sampled from the Abrolhos Islands (Babcock *et al.* unpublished data). In 1988, 387 colonies from at least 51 species were sampled from Ningaloo Reef. As a result of these surveys, most of the coral species that were studied were sampled repeatedly at two or all of these locations.

Table 1

Summary of coral mass spawning observations on Western Australian Reefs during March 1987. Sea temperatures are monthly means from Pearce (1986); tidal data from Easton (1970). (s, semi-diurnal tides; d, mainly diurnal tides; * estimated tide and temperature data).

Location	Latitude (°S)	Tide range (m)	Temperature range (°C)	Dates of main spawning	Nights after full moon
Koolan Is.	16	>10/s	31-24	23, 24	8, 9
Dampier Arch.	20	~ 5/s	30-22	23, 24	8, 9
Lowendal Is.*	20	~ 4/s	30-23	23, 24	8, 9
Ningaloo Reef	23	< 2/s	27-23	23, 24	8, 9
Abrolhos Is.	28-29	~ 1/d	24-20	25, 26	10, 11

Results

Preliminary studies of coral gametogenesis, the results of tagging studies and random surveys in the weeks before and after spawning, as well as direct observations, indicate that most of the corals studied spawned after the full moon in March each year. During some years, however, a small percentage of corals with ripe gonads did not spawn after the March full moon (Simpson 1985). Observations of a small number (<10) of colonies spawning and a small spawn slick at Coral Bay (M Forde, pers. comm) after the full moon in April in 1986 suggest that these corals spawn a month later. Further observations since 1988 indicate that a small percentage of corals (usually less than 10%) spawn after the full moons in February and April each year.

Spawning occurred mainly around 7-9 nights after the full moon during a period of maximum sea temperatures, within 3-4 hours after dark and during neap, ebb tides (Simpson 1985, 1987, 1988). An exception occurred in 1987 at the Abrolhos Islands where spawning occurred mainly on the 10th and 11th nights after the full moon. Direct observations and results from daily monitoring of tagged corals indicated that, in most years, a small percentage of the coral population spawned on one or two nights either side of the main spawning nights (Simpson, unpublished data). Simultaneous observations along the coastline of Western Australia in March 1987 indicated that a high degree of spawning synchrony exists within and between regionally separate coral reefs in Western Australia, and that spawning on these reefs occurred under markedly different environmental conditions

(Table 1). Similar observations in 1988 support these conclusions (Simpson 1987).

A total of at least 165 species of scleractinian corals (41 genera, 13 families) were examined in the periods following the full moon in March between 1985-1988 (Table 2). These studies indicate that at least 102 species of corals that occur on Western Australian reefs shed gametes during a brief, predictable spawning period each year. A further 44 species contained ripe gonads, indicating that spawning was imminent and suggesting that these species also participate in the mass spawning. The total of definite and probable spawning species represents approximately 46% of the 318 species of scleractinian corals, from 70 genera, currently described from Western Australia (Veron & Marsh 1988). A high percentage (88 %) of the coral species that were examined were either definite or probable spawners suggesting that many of the other unexamined coral species that occur on Western Australian reefs are likely to be involved in the annual mass spawning event.

None of the coral species that were examined contained or released planulae during this period and mature gonads were not observed in any corals collected during November 1984 or May to October 1985. In addition, preliminary data on the gametogenic cycle of species of Acroporidae, Faviidae, Mussidae and Oculinidae at Ningaloo Reef between 3 October 1985 and 26 March 1986 suggest that the gametogenic cycles of these species are similar to the same or like species on the Great Barrier Reef (Marshall & Stephenson 1933, Kojis & Quinn 1981, Harriot 1983, Babcock 1984, Wallace 1985) although it is offset by 4-5 months.

Table 2.

Comparison of the number of coral species found to be definite or probable autumn spawners on Western Australian reefs in relation to the total number of species currently known from Western Australia (* from Veron & Marsh 1988) and the number of species examined.

FAMILY	Number of species in Western Australia*	Number of species examined	Number of species that spawned	Number of species with ripe gonads
ASTROCOENIIDAE	2	1	0	0
POCILLOPORIDAE	9	1	0	0
ACROPORIDAE	98	60	50	7
PORITIDAE	30	16	6	7
SIDERASTREIDAE	12	5	0	2
AGARICIIDAE	20	7	1	3
FUNGIIDAE	28	4	1	3
OCULINIDAE	3	2	1	1
PECTINIDAE	11	6	4	2
MUSSIDAE	17	8	4	3
MERULINIDAE	7	6	2	3
FAVIIDAE	59	42	30	9
TRACHYPHYLLIIDAE	2	0	-	-
CARYOPHYLLIIDAE	9	1	1	-
DENDROPHYLLIIDAE	11	6	2	4
TOTAL	318	165	102	44

Reproductive swarmings of polychaete worms, predominantly rag-worms (Polychaeta: Nereidae) but including many other species such as *Eunice cf australis*, occurred simultaneously with the coral mass spawnings in all instances. The epitokous (reproductive) stage of these worms emerged following the onset of coral spawning. Other taxa observed spawning during this period include Alcyonarians and species of Mollusca and Echinodermata (Marsh 1988).

Discussion

There are many similarities between the coral mass spawning events observed on the Great Barrier Reef and on Western Australian reefs. Most species are simultaneous hermaphrodites and spawn after a full moon, over 2 or 3 consecutive nights, during a period of neap tides and within 3 to 4 hours after sunset. Additionally, mass spawning appears to be a predictable, annual event in both locations and approximately 60% of the species observed to spawn or contain ripe gonads in Western Australia mass spawn on the Great Barrier Reef (Harrison *et al.* 1984, Babcock *et al.* 1986, Shlesinger & Loya 1985, Simpson 1985, 1986). The colours, general buoyancy (Babcock *et al.* 1986) and size range of mature eggs (Marshall & Stephenson 1933, Kojis & Quinn 1981, Harriot 1983, Babcock 1984, Wallace 1985) and the most common spawning behaviour are also similar (Babcock *et al.* 1986). The synchronous spawning of corals on regionally separate reefs (Table 1, Babcock *et al.* 1986) and the time between consecutive spring spawnings on the Great

Barrier Reef and autumn spawnings on Western Australian reefs (Willis *et al.* 1985, Babcock *et al.* 1986, Simpson 1988) are further similarities. The remarkable likeness of coral spawning on the east and west coasts of Australia suggests that the same phenomenon is being observed.

Different seasonal timing of mass spawning, and as a consequence, the different environmental conditions that exist during the periods of gametogenesis, spawning, larval development and settlement are the most significant differences between the two locations. For example, mass spawning on the Great Barrier Reef occurs after a period of rapidly rising sea temperatures, although these temperatures are still well below the maxima for these locations (Fig. 2a). In contrast, spawning on Western Australian reefs coincides with the period of maximum seawater temperatures (Fig. 2a, b). There are further differences. Corals on offshore reefs in tropical Western Australia (eg Lowendal Is) spawn at the same time as corals on inshore reefs (eg Dampier Archipelago, Table 1), in contrast to the one month difference that occurs between Magnetic Island and the offshore reefs on the Great Barrier Reef (Babcock *et al.* 1986). Corals on the Great Barrier Reef also spawn around neap tides but, because of the aphasic tides in tropical east Australia, spawning occurs mainly three to six nights after the full moon. As a result, spawning on the Great Barrier Reef occurs before, during and after moonrise (Babcock *et al.* 1986) whereas in Western Australia, corals spawn well before moonrise (Simpson 1985). A further difference is that species of *Turbinaria* participate in the mass spawning

mainly three to six nights after the full moon. As a result, spawning on the Great Barrier Reef occurs before, during and after moonrise (Babcock *et al.* 1986) whereas in Western Australia, corals spawn well before moonrise (Simpson 1985). A further difference is that species of *Turbinaria* participate in the mass spawning event in Western Australia but not on the Great Barrier Reef where spawning of this genus occurs in autumn (Harrison *et al.* 1984). These differences possibly reflect adaptation to local conditions.

Coral mass spawning on Western Australian reefs coincides approximately with the annual intensification of the Leeuwin Current, a warm poleward current of tropical origin that flows unidirectionally along the Western Australian coastline in autumn and winter (Cresswell & Golding 1980, Godfrey & Ridgway 1985). This current flows predominantly, but not exclusively, during the austral autumn and winter and provides a mechanism for the southward dispersal of coral planulae which, in turn, raises the possibility of a unidirectional gene flow between regionally separate coral reefs in Western Australia.

The reproductive cycles of marine invertebrates are considered to be influenced predominantly by temperature (Orton 1920, Giese & Pearse 1974) and this factor has been suggested as having an important influence in timing the gametogenic cycle of scleractinian corals (Harrison *et al.* 1984, Babcock *et al.* 1986, Oliver *et al.* 1988, Richmond & Hunter 1990). Furthermore, differences in temperature patterns have been suggested as possible explanations for observed differences in the timing of coral spawning on the northern (Harriot 1983) and southern (Kojis & Quinn 1981) Great Barrier Reef and between the onshore and offshore reefs on the central Great Barrier Reef (Babcock *et al.* 1986). Seawater temperatures at the Dampier Archipelago show a pronounced seasonal pattern and are similar to sea temperatures at Magnetic Island, yet the breeding seasons of corals at these two locations are about 5 months apart (Fig. 2a). In contrast, sea temperature patterns along the Western Australian coastline are quantitatively and qualitatively different due to the varying influence of the Leeuwin Current, yet mass spawning occurs synchronously between regionally separate reefs (Fig. 2b, Table 1) and between onshore and offshore reefs (Table 1). These data suggest that sea temperature is not a universal proximate cue or ultimate factor in determining the timing of the breeding season of scleractinian corals.

An alternative hypothesis is that the breeding season of corals in Australia is not controlled by environmental cues but is the result of an endogenous rhythm which reflects historical breeding patterns of ancestral corals (Simpson 1987, 1988) and has been termed the Genetic Legacy Hypothesis by Oliver *et al.* (1988). Ocean circulation patterns at the time of coral spawning on the east and west coasts of Australia and preliminary data on the breeding season of corals in

equatorial regions support this hypothesis. Mass spawning of corals occurs in late spring/early summer on the Great Barrier Reef and during autumn on Western Australian reefs. In both locations spawning coincides approximately with the annual change from a northerly or variable net drift to a pronounced net southerly drift of surface waters (Fig. 1) and with periods of calms associated with the seasonal changes in monsoonal wind patterns (Pickard *et al.* 1977, Williams *et al.* 1984, Holloway & Nye 1985). The southerly drift of tropical water along the Great Barrier Reef originates from the South Equatorial Current and occurs during late spring and summer whereas during autumn and winter surface waters of the Great Barrier Reef drift northward under the influence of the south-east trade winds. Off Western Australia the opposite situation exists. The Leeuwin Current, originating as inflow from the Western Pacific to the Indian Ocean through the Indonesian Archipelago (Godfrey & Ridgway 1985), flows strongly southward along the coastline during autumn and winter. Weaker flows and periodic reversals occur during late spring and summer when south-westerly winds predominate. Thus, in both areas, albeit in different seasons, a mechanism exists for the southward transport of coral larvae from equatorial regions.

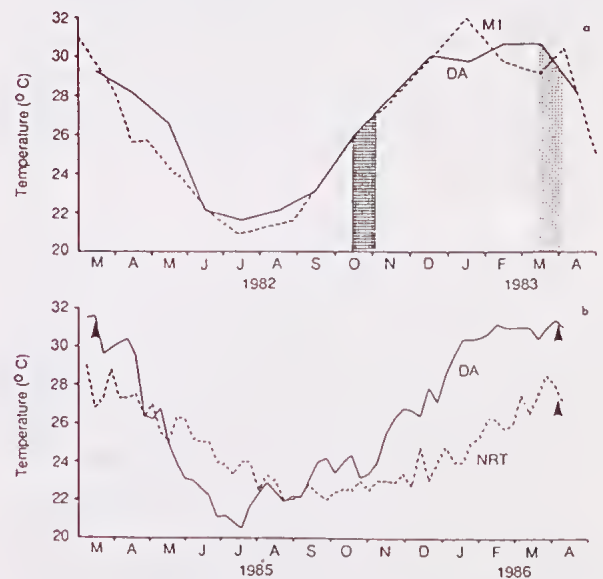


Figure 2 (a) Annual seawater temperature patterns and asynchronous breeding seasons of corals at Magnetic Island (MI, dark shade) and the Dampier Archipelago (DA, light shade); (b) annual seawater temperature patterns and synchronous periods of coral mass spawning (arrows) at the Dampier Archipelago (DA) and the Ningaloo Reef tract (NRT). Data for the Dampier Archipelago for (a) from monthly means and (b) from weekly means. Data for Magnetic Island from Babcock *et al.* (1986) and for the Ningaloo Reef from weekly means.

Preliminary studies of coral reproduction in equatorial regions have shown that the breeding season of several coral species extends from approximately September to March (Oliver *et al.* 1988). The same species are known to spawn in spring on the Great Barrier Reef and in autumn on Western Australian reefs. Thus as a result of this extended breeding season and the seasonal difference in the flow of tropical water down the east and west coasts of Australia, coral larvae produced in equatorial regions during the austral spring and summer are more likely to be transported to the east coast of Australia than to the west coast. Similarly, larvae produced in equatorial regions during the austral autumn are more likely to be transported to the west coast of Australia than the east coast. If this is the case, the different spawning seasons of corals on the east and west coasts of Australia may well be a reflection of ancestral breeding patterns and be the result of selective dispersal of coral larvae from equatorial populations that have extended breeding seasons. However, as Oliver *et al.* (1988) point out, this hypothesis would be weakened if corals from equatorial regions spawned more than once a year. Although their study in Papua New Guinea indicated that some individual corals had ripe gonads in September-November and January-March, suggesting two gametogenic cycles and, therefore two spawning periods, this has yet to be proven specifically or generally. A common origin would explain the remarkable similarity in many of the reproductive traits observed in corals on the east and west coasts of Australia. Furthermore, an endogenous rhythm would also explain the latitudinal synchrony of coral spawning on reefs with markedly different environmental conditions (Table 1).

Within the breeding season, corals on the east and west coasts of Australia appear to respond to lunar/tidal patterns and light/dark cycles as proximate cues for spawning synchrony (Babcock *et al.* 1986, Simpson 1988). The variation in the time of spawning within the respective breeding seasons on the east and west coasts of Australia (eg different nights after the full moon), is probably the result of local adaptation.

At present the mass spawning of scleractinian corals has been recorded only on the east and west coasts of Australia. Mass spawning does not appear to occur in the Caribbean Sea (Szmant-Froelich *et al.* 1984) or in the Red Sea (Shlesinger & Loya 1985). A suggested explanation is that environmental conditions at these locations are less extreme than on the Great Barrier Reef (Shlesinger & Loya 1985). The data presented here suggest this is not the case, as tides and sea temperatures vary markedly, both qualitatively and quantitatively, along the Western Australian coastline yet mass spawning occurs synchronously. In contrast, tides and sea temperatures at Magnetic Island and at the Dampier Archipelago are similar yet mass spawning is about 5 months out of phase. Why corals exhibit reproductive traits as diverse as temporal

reproductive isolation and synchronous multispecific spawning is not clear. Perhaps the reproductive patterns of Red Sea corals are indeed adaptations to an unstable environment that has occurred throughout their evolutionary history (Shlesinger & Loya 1985) or perhaps it is merely a reflection of their 'diffuse' origin. The similarity of coral mass spawning on the east and west coasts of Australia suggests that multispecific, synchronous spawning during brief, annual periods may be a common reproductive pattern for reef corals. Whether this reproductive pattern is confined to non-equatorial coral populations that are genetically 'connected' to equatorial coral populations by ocean currents remains to be seen.

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